Pacific Science (1999), vol. 53, no. 3: 273–285

Botany and Genetics of New Caledonian Wild Taro, *Colocasia esculenta*[1]

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ABSTRACT: Taro, *Colocasia esculenta* (L.) Schott, is considered to be an introduced crop in New Caledonia and has been cultivated since its introduction by Melanesian farmers. Wild germplasm exists on the main (continental) island and is represented by three easily distinguished morphotypes: a morphotype with purple leaves, another with green leaves, and a third with green leaves and a purple vein junction on the lamina. All three morphotypes are diploids ($2n = 2x = 28$) and have well-established wild populations in many valleys and gulches of the main island. The morphotype with purple leaves has all typical traits of a wild genotype (inedible corms; long, thin stolons); the other two produce edible corms. The purple and the green morphotypes flower and produce fertile pollen. The spathes of the green morphotype can be more than 40 cm long and the spadix is characterized by an extremely long appendix atypical for Pacific taros. Isozyme analysis conducted using four enzyme systems (EST, PGM, PGI, SkDH) indicated that New Caledonian wild taros differ from most widely grown local cultivars and Pacific cultivated and wild genotypes. Evidence presented in this study suggests that *C. esculenta* is an endemic species to New Caledonia. Cultivars were probably introduced as clones from what is now Vanuatu by early Melanesian migrants and were not domesticated locally from existing wild forms, which appear to be genetically distant from other Melanesian wild taros.

TARO, *Colocasia esculenta* (L.) Schott, is a vegetatively propagated root crop species of the monocotyledonous family Araceae and is grown in almost all tropical regions of the world. It is generally believed that this species originated in Indo-Malaya although there is insufficient evidence. Taro's center(s) of origin, spread, and domestication have been studied by several authors (Spier 1951, Yen and Wheeler 1968, Plucknett 1984, Jones and Meehan 1989, Matthews 1990, Lebot and Aradhya 1991, Lebot 1992). It is possible that the center will never be found because much genetic evidence has already been lost. Many cultivars have disappeared or transferred to different places, and many wild populations have been destroyed by intense agricultural practices.

The origin of wild germplasm in some Pacific countries (Australia, Papua New Guinea, the Solomons, and Vanuatu) is also controversial. If taro was brought to these countries it was probably brought in a cultivated and not in a wild form. It is unlikely that migrating people collected and distributed wild genotypes that had inedible corms with very high concentration of oxalates. Wild germplasm has not been studied thoroughly. Breeders have avoided wild genotypes because of their many negative characteristics. In the future, however, wild genotypes may become an important source of genes for the improvement of resistance and/or tolerance to pests and diseases, adaptability to extreme drought or paddy environment, earliness, long growth period, and other characteristics.

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Wild taro populations can be found almost everywhere in the lowlands of New Caledonia, except in saline soils. They can survive long periods of drought and their recovery during the rainy season is spectacular. Wild genotypes may have been introduced to some countries by birds eating taro seeds (Hambali 1980), but probably not to New Caledonia because of its isolation. New Caledonia was formed on a ridge situated between the Sahul continent and the eastern active islands of Melanesia. The formation of the current ridge began on the outer margin of Gondwanaland before the Permian, 280 million yr ago (Paris 1981). New Caledonia appears to be geographically isolated from the taro's center(s) of origin, and therefore the problem of the origin of its wild populations is an interesting phylogenetic and evolutionary question.

Taro is considered to be an introduced crop to New Caledonia (MacKee 1985), probably from what is now Vanuatu (Virot 1956). Lebot and Aradhya (1991), using isozymes as molecular markers, investigated local cultivars and found zymotypes identical or very similar to those of the other Pacific taros. Unfortunately, their study did not include wild genotypes. The investigation reported here was partly inspired by oral reports of local agronomists and anthropologists regarding the existence of an unknown, vigorous wild *Colocasia* species growing on the east coast of the main island (Grande Terre). In the newer literature about the New Caledonian flora, the genus *Colocasia* is represented by only one species: *C. esculenta.* In older literature, however, Guillaumin (1948) mentioned *Colocasia neo-caledonica* as a nomen nudum of a totally unknown species, but failed to give any further explanation.

The objectives of this study were to characterize New Caledonian taro populations and to study their morphological and genetic variability, genetic relationships with cultivated varieties, reproduction systems, adaptability, and breeding value. Another objective was to elucidate their origin: are they true wild genotypes endemic to New Caledonia or "escapes" from cultivation (feral taros) and related to other Pacific genotypes.

MATERIALS AND METHODS

Morphological Variation

According to Melanesian elders, the "true" wild taro could be found only on Grande Terre. They divided wild taro genotypes into two groups: "dark" (which could be found throughout Grande Terre) and "green" (which could be found only in limited areas of the east coast). We decided to conduct a preliminary study of morphological variation and reproduction systems (flowering, pollination systems, fertilization, propagation by seeds, and vegetative propagation) in the natural environment and to collect samples for further systematic investigation.

Based on morphological characteristics, such as leaf pigmentation, pigmentation of the vein junction on the leaf blade, corm shape, and characteristics of stolons, the accessions were separated into three distinct morphotypes: "purple," "green," and "green with a purple vein junction on the lamina" (having a distinct purple marking 4–10 cm long with a "Y" shape). The last morphotype is referred to hereafter as "purple-green." A sample from all three morphotypes was planted in an experimental plot at the CIRAD Research Center at Pouembout (northwestern part of Grande Terre). Half of the accessions were treated with a flower-inducing hormone (aqueous solution of gibberellic acid: 0.4–0.5 g liter^{-1}) to produce simultaneous flowering needed for studying pollination mechanisms, fertilization, and (in)compatibility systems. Another sample from each morphotype was taken to the laboratory and kept in buckets of water for chromosome counts. Corms of the collected plants were used for estimation of eating quality, judged by tasting young, semimature, and mature corms cooked in the same way as the corms of cultivars.

Morphological variation was scored for the following traits: presence/absence of stolons, corm characteristics, plant height, leaf lamina dimensions, incidence of natural flowering, and characteristics of inflorescence. Data collection took place in the three largest and most uniform populations in the north-

eastern part of Grande Terre: one in the Tiwaka Valley (the purple morphotype) and two in the Tchamba Valley (the green and the purple-green morphotypes). Morphological characteristics also included two traditional New Caledonian cultivars grown on a multiplication plot at Wagap: cv. Matéo Rose and cv. Païta (Wagap is situated on the coast between the Tiwaka and Tchamba Valleys).

Reproductive Biology

Reproduction systems, incidence of flowering, self-pollination, cross-pollination, vectors of pollination, and self-(in)compatibility were studied in natural environments (in the three locations mentioned above and along small rivers around Pouembout) and on two irrigated experimental plots (one on the east coast, the other on the west coast) planted together with traditional cultivars and artificial hybrids introduced from CIRAD greenhouses in France. Because nothing was known about vectors of pollination and no pollinators had been observed in the preliminary investigation, we decided to plant several plant species attractive to insect pollinators, such as *Cucurbita pepo*, *C. maxima*, *Cucumis melo*, *C. sativus*, *Pisum sativum*, and *Vicia faba*, around the taro experimental plots at Pouembout. We hoped to attract as many insect species as possible, among which some might pollinate taro.

Self-(in)compatibility was studied under controlled conditions (self-pollinations in artificial isolation) and in natural environments (by observing natural seed set and development of fruit clusters). Cross-(in)compatibility was studied only under controlled conditions, and inflorescences were emasculated, crossed, and isolated by cotton wool. Some wild plants were used as female parents and some as males. Pollen fertility was determined indirectly, with a light microscope, using Alexander's solution for coloring (Jahier et al. 1992), and directly by using it in hybridization. Inflorescences for analysis of pollen viability of the purple morphotype were collected on vigorous plants growing along one of the small rivers near Pouembout. Pollen, taken from five inflorescences, was put on a white sheet of paper, mixed together, and put in a dark cupboard inside a laboratory with temperature varying from 20 to 25°C. Each day pollen was mixed again and a sample was taken for analysis of viability. Every few days another sample from the same pollen source was used for pollination of two inflorescences on vigorously growing hybrids.

Chromosome Counts

Determination of chromosome numbers was based on protocols described by Coates et al. (1988) and Matthews et al. (1992), but pretreatment was modified using a 0.04% solution of 8-hydroxyquinoline rather than a 0.2% aqueous solution of colchicine. Root tips were immersed in the solution of 8-hydroxyquinoline at room temperature for 3 hr, then fixed in 3 : 1 ethanol and acetic acid at 4°C overnight. Root tips stained by Feulgen's solution were hydrolyzed for 4 min in 1M HCl at 60°C and squashed on a slide in a saturated solution of aceto-carmine and 45% acetic acid.

Isozyme Variation

This isozyme analysis is an addition to Lebot and Aradhya's (1991) geographical survey that appraised isozyme variation among 87 cultivars from New Caledonia. This analysis includes the two most widely grown cultivars, 'Wallis' and 'Kary', which were used as controls (local checks) because they are representatives of typical New Caledonia and Pacific taros. Their zymotypes were compared with those of the wild forms.

Several enzyme systems were assayed using a variety of buffer systems, but only histidine citrate, pH 6.5, was found to be useful. The tray buffer was histidine-free base (0.065 M) and citric acid anhydrous (0.007 M); the gel buffer was histidine (0.016 M) and citric acid (0.002 M). Leaf extracts were obtained using the buffer protocol described by Lebot and Aradhya (1991). Samples were electrophoresed at 4°C. Running conditions were 15 V/cm and 50 mA for

FIGURE 1. Wild taro (green morphotype) growing on a lowland pasture in Tchamba Valley, east coast of New Caledonia.

6 hr. Four enzymatic systems were stained successfully, and clear banding patterns were revealed. After electrophoresis, the gels were sliced horizontally and stained for peroxidase (PER), esterase (EST), shikimic-dehydrogenase (SkDH), and phosphoglucomutase (PGM). Electromorphs were used as isozymic descriptors and each electromorph was considered as a character, with presence scored 1 and absence scored 0. A total of 16 electromorphs was used as enzymatic descriptors and if two accessions were different for at least one electromorph (present or absent), they were considered to exhibit two different zymotypes. Multivariate relationships among zymotypes were appraised using the simple matching coefficient and cluster analysis (UPGMA) on the matrix OTUs × electromorphs. These computations were expedited by using the NTSYS program (Exeter Publishing Ltd., Setauket, New York).

RESULTS

Morphological Characteristics

All three wild morphotypes (purple, green, and purple-green) appear to be well adapted to their environments and stable members of existing plant communities. They can be found along rivers, in swampy areas, in lowland pastures (Figure 1) and grasslands, and around gardens. They grow well in intensely used wet lowland pastures because cattle, which avoid taro plants, provide a sort of weed control. Grasses efficiently protect the soil from excessive solar radiation and evaporation. In areas where there are no cattle, taro plants grow in smaller and dense groups, or subpopulations, and usually compete efficiently with the aggressive growth of grasses and other species.

Populations with more than 10,000 individuals are rare and are usually split into

TABLE 1

MORPHOLOGICAL CHARACTERISTICS OF NEW CALEDONIAN WILD TAROS AND TWO LOCAL CULTIVARS (MEASURED IN FEBRUARY 1998)

CHARACTERISTIC/GENOTYPE	*n*	MEAN	CV (%)	MIN.	MAX.
Plant height (cm)					
'Matéo Rose'	30	101.64	8.19	88.0	119.0
'Païta'	30	89.14	14.45	63.2	111.9
Purple	40	109.66	9.85	94.0	150.9
Green	30	141.52	8.37	127.5	159.2
Purple-green	30	97.72	11.21	76.6	115.8
Number of functional leaves of the main stem					
'Matéo Rose'	30	6.87	14.70	5	9
'Païta'	30	5.83	12.86	5	7
Purple	40	2.77	17.33	2	4
Green	30	4.40	11.36	4	5
Purple-green	30	2.47	25.51	1	4
Lamina length of the tallest leaf (cm)					
'Matéo Rose'	30	42.52	10.70	31.3	47.2
'Païta'	30	34.97	15.36	22.6	43.0
Purple	40	36.47	8.31	32.2	42.1
Green	30	81.32	9.49	64.5	93.7
Purple-green	30	43.09	13.04	30.9	52.8
'Inrin Diawe'	15	24.04	11.52	19.1	28.5
Lamina width (cm)					
'Matéo Rose'	30	32.32	9.59	26.2	37.4
'Païta'	30	25.31	19.56	16.0	38.1
Purple	40	23.24	7.44	20.2	25.6
Green	30	62.04	9.12	51.4	69.4
Purple-green	30	31.42	14.35	22.3	39.1
'Inrin Diawe'	15	22.62	10.83	18.5	26.5
Lamina width: lamina length (ratio)					
'Matéo Rose'	30	0.76	7.50	0.67	0.93
Païta	30	0.72	8.89	0.63	0.97
Purple	40	0.64	2.97	0.59	0.68
Green	30	0.76	4.74	0.64	0.82
Purple-green	30	0.73	4.25	0.67	0.79
'Inrin Diawe'	15	0.94	6.06	0.85	1.01

subpopulations. One was found in the Tchamba Valley and another in the Nimbaye Valley on the east coast of Grande Terre. In vigorous and stable subpopulations, which may contain from 50 to 2500 individual plants, the number of plants per square meter varies from 8 to more than 15. In populations along rivers, the density frequently exceeds 25 plants per square meter. One of the consequences of high density is the low number of functional leaves per plant (Table 1).

The purple morphotype can be found almost everywhere on the main island, but the other two are distributed mainly on the east coast, which is more humid, being on the windward side of the island. All three morphotypes rarely appear together in one population. The purple and the green morphotypes can be found together in the Nimbaye Valley (south of the Tchamba Valley), but usually form separate subpopulations. In the Tchamba Valley, the green morphotype grows together in a mixed population with the purple-green one. The green morphotype usually dominates because the plants are taller and the leaves larger.

All studied wild morphotypes are dasheen types with well-developed central corm and small or no side cormels. The purple and the purple-green morphotypes produce long, thin stolons; the green morphotype produces cylindrical suckers, which can also be described as short (3–10 cm long), thick (1.7–2.5 cm in diameter) stolons. Such structures have never been described before and are similar to the cormels of *Xanthosoma sagittifolium* but they never tuberize.

The plants of the green morphotype are the tallest, with the largest leaves. The average lamina length, measured on the tallest leaf, is 81.32 cm and the maximum value is 93.7 cm (Table 1), measured in the Tchamba Valley during the wet season (February 1998). These are probably among the highest values ever recorded for *Colocasia esculenta.* For comparison, the length of the largest leaves measured by Ivancic et al. (1995) in Papua New Guinea did not exceed 90 cm.

The shape of leaves, expressed as the ratio between lamina width and lamina length, was found to be different from the shape of leaves of the oldest traditional New Caledonia cultivars, which were characterized by almost round leaves. One of the examples kept in the CIRAD germplasm collection at Wagap is cv. Inrin Diawe, with an average ratio of 0.94 (Table 1).

During the dry, cool period (from May to October) leaves disappear completely, and grasses or other plants can cover the taro. However, the rains and increasing temperature at the end of the year cause a quick recovery of the taro plants, and they soon become dominant members of plant communities and some plants start flowering.

Corms of the purple and the green morphotypes can be relatively large and their weight can exceed 2 kg. The corms of the purple-green morphotype are smaller and elongated. Shape, however, depends strongly on location, environmental conditions, and plant age. Some of the plants may be 2 yr old, as ascertained from the corm surface, on which can be clearly distinguished the effects of the rainy and dry seasons and residuals of floral clusters.

Palatability tests clearly showed that the corms of the purple morphotype were not edible because of undesired texture and high concentration of oxalates, but corms of the other two could be used as food for humans. Their eating quality, however, was poorer than that of the most desired cultivars such as 'Wallis', 'Kary', 'Bourbon', 'Païta', or 'Matéo Rose'. It was also found that the corms of wild genotypes could not be used as food at all times of the year. The best corms were harvested at the end of the growing season from 1-yr-old plants grown on fertile, not swampy soil and not in a completely shaded area. The corms had to be left for a few days in a dry, cool place to get rid of excess water and had to be boiled a bit longer than the corms of cultivars.

Reproductive Biology

INCIDENCE OF FLOWERING AND FLORAL MORPHOLOGY. The first inflorescences appeared on the purple morphotype at the beginning of February 1998 and were synchronized on the east and west coasts. The green morphotype started to flower about 3 weeks later, but the purple-green morphotype was not seen to flower, not even after the treatment with gibberellic acid.

The proportion of flowering plants within the populations of the purple morphotype varied from 3 to 15%, depending on location. Plants usually developed only one floral cluster of three to five inflorescences with long, dark yellow spathes on long peduncles (Figure 2). The incidence of flowering within the populations of the green morphotype was generally much lower; only 0.5–4% of plants were flowering, developing one floral cluster with two to four or rarely five inflorescences. Hybrids developed many more inflorescences per plant. The highest number per plant recorded in the Wagap germplasm collection was 27 inflorescences, distributed in nine floral clusters.

Inflorescences of the green morphotype were much larger than those of the purple one (Table 2). The longest spathe was 44.20 cm, and the longest spadix was 28.50 cm. One of the most discriminant characteristics of the two flowering wild morphotypes was the

FIGURE 2. Flowering plants of cultivated and wild New Caledonian taro: (1) cultivar Matéo Rose; (2) purple morphotype of wild taro.

length of the sterile appendix (Figure 3). In both of them its average length was longer than the length of the male portion (Table 2). This was remarkable on the inflorescences of the green morphotype, where the average ratio between the length of the sterile appendix and the length of the male portion was 1.50. The Pacific taros we observed in germplasm collections in Hawai'i, Papua New Guinea, the Solomon Islands, Vanuatu, and Western Samoa exhibited relatively short appendices. The same observation is valid for wild types existing in these countries.

POLLINATION AND FERTILIZATION. Flowering of the purple and the green morphotypes was open (Figure 3 [2–4]). The opening of the upper part of the spathe of the purple morphotype was wide enough to enable large insects, even larger than honey bees, to reach the male portion. The spathes of the green morphotype opened completely. Spathes of all inflorescences were in a drooping position during anthesis, and pollen released from such inflorescences could be spread by wind. The shortest time period from the first appearance of the spathe tip from the petiole sheath to the moment when pollen was released was 8 days and was observed in populations of the purple morphotype. On sunny days, in vigorous populations along rivers, pollen appeared before 0800 hours, but in drier places pollen could be seen after 1000 hours.

Preliminary experimentation with hybridization indicated that protection of a pollinated inflorescence by cotton wool was essential for successful fertilization and fruit development because of the windy, dry weather. Viability of fresh pollen of the purple morphotype, determined by Alexander's stain, varied from 36.57 to 88.95%. Viability of pollen of the green morphotype was 68.22%. Viability of pollen of the hybrids varied from 64.35 to 93.31%, and a sample of the local cultivar 'Wallis' had 80.96% viable pollen. Pollen of the purple morphotype left on the inflorescence lost viability quickly.

TABLE 2

MAIN FLORAL CHARACTERISTICS OF NEW CALEDONIAN WILD TAROS AND TWO LOCAL CULTIVARS (MEASURED IN FEBRUARY 1998)

CHARACTERISTIC/GENOTYPE	*n*	MEAN	CV (%)	MIN.	MAX.
Length of the spathe (cm)					
'Matéo Rose'	29	30.46	8.34	26.10	35.70
'Païta'	25	26.84	15.05	18.60	34.45
Purple	25	29.26	13.23	22.10	37.60
Green	30	38.45	8.89	32.20	44.20
Length of the spadix (cm)					
'Matéo Rose'	29	9.88	6.78	8.20	10.81
'Païta'	25	9.35	9.95	7.61	10.90
Purple	25	13.20	9.70	11.10	15.60
Green	30	25.07	7.62	21.00	28.50
Length of the female portion (cm)					
'Matéo Rose'	29	3.12	6.73	2.70	3.60
'Païta'	25	2.83	13.07	2.30	3.45
Purple	25	3.43	13.99	2.60	4.50
Green	30	5.25	12.00	4.30	6.10
Length of the male portion (cm)					
'Matéo Rose'	29	3.90	8.46	3.20	4.40
'Païta'	25	3.58	8.66	3.10	4.20
Purple	25	3.96	9.59	3.20	4.50
Green	30	6.64	10.09	5.10	8.30
Length of the sterile appendix (cm)					
'Matéo Rose'	29	0.93	16.13	0.70	1.20
'Païta'	25	1.09	19.27	0.70	1.40
Purple	25	4.02	12.93	3.40	5.10
Green	30	9.95	10.05	7.50	11.30
Sterile appendix: male portion (ratio of lengths)					
'Matéo Rose'	29	0.24	12.08	0.19	0.30
'Païta'	25	0.30	17.33	0.21	0.39
Purple	25	1.01	7.82	0.87	1.17
Green	30	1.50	6.00	1.26	1.68
Number of fertile female flowers on female portion					
'Matéo Rose'	29	201.79	12.44	158	236
'Païta'	25	203.44	12.66	122	252
Purple	25	221.92	16.30	176	320
Green	30	265.50	11.12	216	335
Number of pistoids: number of fertile female flowers (ratio)					
'Matéo Rose'	29	0.15	18.00	0.11	0.19
'Païta'	25	0.25	20.40	0.20	0.38
Purple	25	0.14	43.57	0.06	0.19
Green	30	0.49	12.24	0.36	0.6

Viability was 56.37% 36 hr after pollen had been released (28 February 1998). Two days later (2 March) it was 19.13%, and the following day viability was only 3.88%. On 4 March, further estimation was no longer possible because fungi had destroyed the pollen.

Pollen of the purple morphotype kept on a sheet of paper inside the laboratory remained above 50% fertile for 21 days. On 23 Febru-

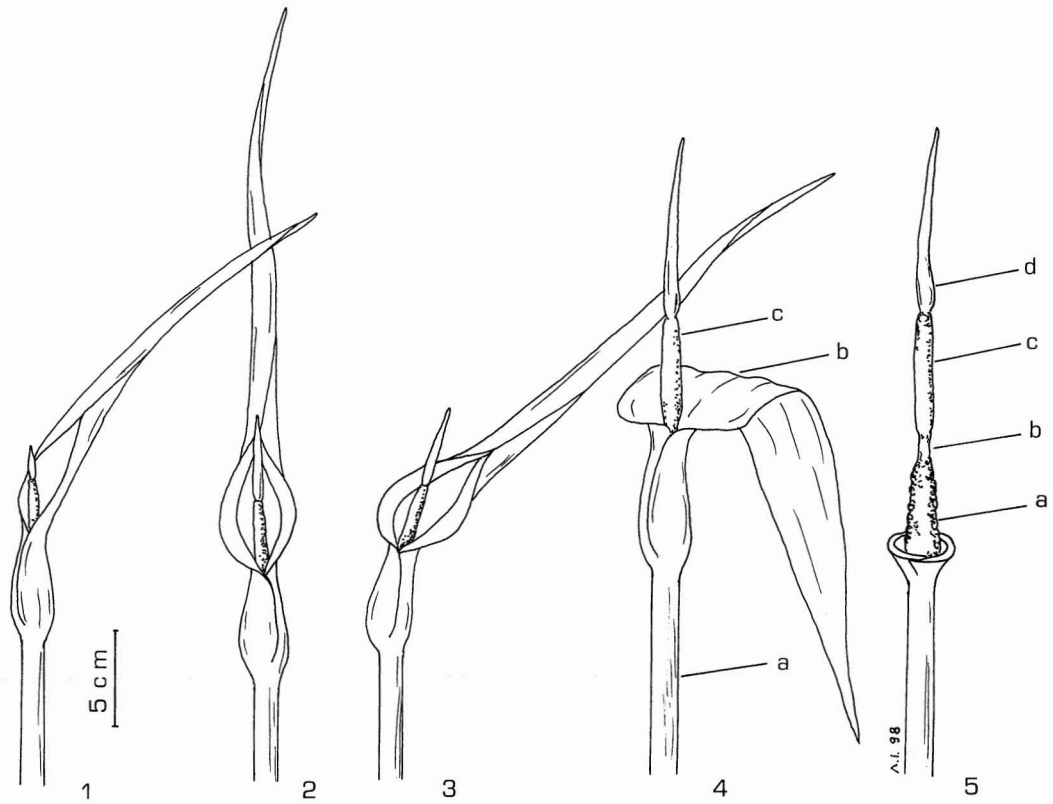

FIGURE 3. Inflorescences of cultivated and wild New Caledonian taro on a day when pollen is released: (1) cultivar Matéo Rose; (2) erect inflorescence of the purple wild type; (3) semierect inflorescence of the purple wild morphotype; (4) fully open inflorescence of the green wild morphotype: (a) peduncle, (b) spathe, (c) spadix; (5) spadix of the green wild type: (a) female portion, (b) neutral region, (c) male portion, (d) sterile appendix.

ary, when it was collected, fertility was 74.87% and on 17 March (after 22 days), the fertility had declined to 47.78%. When 22-day-old pollen was used in hybridization, no seeds were obtained. The oldest pollen that was used successfully for hybridization had been stored for 18 days. Such a long viability of taro pollen enables its transfer anywhere in the world. Because of dangerous viral diseases such as the Alomae-Bobone virus complex, the transfer of pollen might be much safer than the transfer of seeds or even tissue culture. Pollen transfer from resistant genotypes might be useful for international breeding programs aimed at leaf blight (*Phytophthora colocasiae*) resistance.

Taro is an entomophilous species, and the pungent odor of the inflorescences attracts insects. Pollinators found on wild and cultivated taros in New Caledonia belonged to the family Halictidae, endemic to Australia and New Caledonia (S. Chazeau, 1998, pers. comm.). Odorous spathes frequently attracted several other species of insects, especially flies and beetles, which were not found to transfer pollen.

Halictidae are relatively small (in average about 5 mm long) and easily could be confused with smaller flies. In the isolated experimental plot at Pouembout, they appeared about 1 month after flowering started. Their number increased constantly, and within 2 weeks it was possible to find two to three insects per pollinating inflorescence (the total number of flowering plants was 82). None of these insects was found on other flowering

TABLE 3

NATURAL POLLINATION AND FERTILIZATION OF 17 RANDOMLY CHOSEN INFLORESCENCES OF THE NEW CALEDONIAN WILD TARO (PURPLE MORPHOTYPE) AND HYBRIDS

WILD TARO (NATURALLY GROWN POPULATIONS NEAR POUEMBOUT)[a]				HYBRID PLANTS (CIRAD RESEARCH CENTER, POUEMBOUT)[a]			
NO.	*n*	BERRIES	%	NO.	*n*	BERRIES	%
1	272	0	0	1	252	46	18.25
2	184	0	0	2	306	0	0
3	244	0	0	3	276	7	2.54
4	236	0	0	4	305	0	0
5	239	0	0	5	216	8	3.70
6	236	0	0	6	297	2	0.67
7	232	2	0.86	7	307	16	5.21
8	184	0	0	8	372	37	9.95
9	185	0	0	9	359	2	0.56
10	236	0	0	10	296	21	7.09
11	232	0	0	11	255	5	1.96
12	168	0	0	12	435	34	7.82
13	208	0	0	13	299	0	0
14	204	0	0	14	307	16	5.21
15	231	0	0	15	249	0	0
16	212	0	0	16	282	0	0
17	219	0	0	17	216	2	0.92

[a]no., sample number; *n*, total number of fertile female flowers; berries, number of developing berries within the fruit cluster (as an indication of a successful fertilization) determined about 2 weeks after natural pollination; %, percentage of developing berries within the fruit cluster.

species such as pumpkins, melons, watermelons, cucumbers, and beans that were growing around the experimental plot. In natural populations, Halictidae were found on flowering taros almost everywhere, but their number was generally not high.

Halictidae, however, were not found to be successful pollinators. No natural seed set has been observed. Only two developing berries were found on one fruit cluster of the purple morphotype grown in natural environment and a few on hybrids grown in the experimental field at Pouembout (Table 3). The majority of hybrids were found to be self-compatible, and most of the flowering plants had indications of successful fertilization (developing berries within fruit clusters).

Chromosome Numbers

The number of chromosomes was determined on all wild morphotypes. All of them had $2n = 28$ chromosomes. This indicates that they are diploids (the basic number of chromosomes is considered to be $x = 14$). Cultivars Matéo Rose, Païta, Wallis, and Inrin Diawe (a representative of the oldest New Caledonian cultivars) had the same number of chromosomes. These chromosome numbers were expected because 94% of the accessions of the CIRAD germplasm collection at Wagap were flowering (naturally or after being treated with gibberellic acid). According to Yen and Wheeler (1968), Kurvilla and Singh (1981), Coates et al. (1988), and Matthews (1990), the majority of Pacific genotypes should be diploids, with most of the triploids existing in Asia.

Isozyme Variation

The genetic interpretation is complex, and the numerous bands (Figure 4 [1]) are encoded by an unknown number of genes. Zymograms indicate that the wild genotypes exhibit unique electromorphs that do not exist in the investigated cultivar zymotypes, 'Wallis' and 'Kary', which are representatives

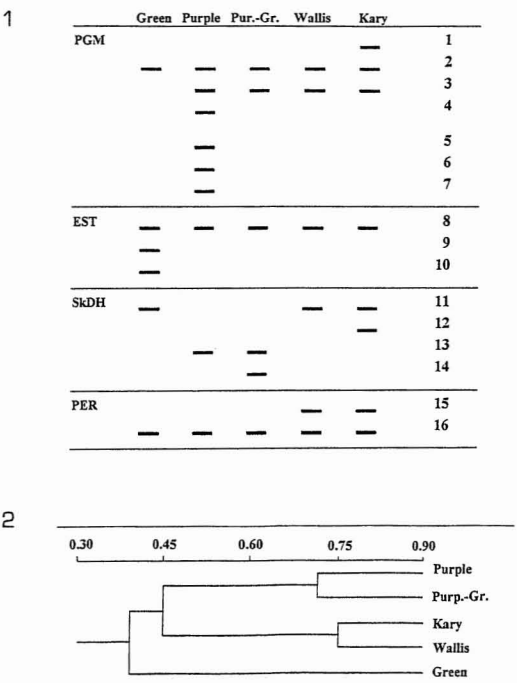

FIGURE 4. (1) Zymograms observed for each enzyme system; (2) UPGMA cluster analysis based on Jaccard's coefficient of similarity among taro zymotypes. Similarity is based on the presence or absence of isozyme bands.

of the most widely grown New Caledonian and Pacific taros (Lebot and Aradhya 1991). Most of the New Caledonian cultivars exhibit identical isozyme patterns.

Zymotypes of the three wild morphotypes were compared with those of the cultivars and the data constituted by the matrix zymotypes × electromorphs were subjected to cluster analysis (Figure 4 [2]). The information gained was also used to identify groups in the distribution of zymotypes on planes (axes 1 and 2) of the principal components analysis to confirm groupings revealed by the dendrogram. All cultivars cluster together and were significantly different from the three wild morphotypes.

DISCUSSION AND CONCLUSIONS

Wild taro germplasm is represented in New Caledonia by three distinct morphotypes. The purple type is spread all across Grande Terre, but the other two are found in limited areas of the east coast. All of them are well adapted to the specific New Caledonian climate, which is characterized by long dry and relatively short rainy seasons, and a sequence of dry, cool periods. Flowering plants can be found only in populations of the purple and the green morphotypes. The green type develops very long inflorescences with a spathe that exceeds 40 cm, and the spadix, characterized by an extremely long sterile appendix, can be up to 28 cm long.

New Caledonian wild taro plants exhibit the typical characteristics of the *esculenta* group: well-developed main corm and small or no cormels. However, analysis of inflorescences showed that the purple and the green morphotypes have appendices that are longer than the male portions. Therefore, according to the existing taxonomy (Purseglove 1979, Plucknett 1983), these obviously *esculenta* types should belong to the *antiquorum* group. This contradiction indicates that the length of the sterile appendix may not be the most appropriate or the absolute character for the distinction between the *esculenta* and *antiquorum* groups, if these groups really correspond to different taxa.

The eating quality and the production of stolons or suckers suggest that the purple morphotype might be the only representative of the true wild germplasm, and the green and the purple-green morphotypes might be ferals. The green morphotype is frequently used as a source of food after cyclones. It cannot be found in taro fields, but in some villages it is grown in backyards as an ornamental. There is no obvious reason why these two morphotypes would have been introduced to New Caledonia because they are hardly edible. It is unlikely that they result from recent introductions because they are widely spread in the wild, where they form stable populations. They could also be true wild genotype with acceptable corm characteristics and, therefore, potential genotypes for domestication.

There are several possible reasons for the absence of natural seed set of wild taro: insects are too large to enter the female

TABLE 4

SELF AND CROSS-(IN)COMPATIBILITY OF NEW CALEDONIAN WILD TARO (PURPLE MORPHOTYPE [WPM]) STUDIED DURING RAINY SEASON IN 1998

SELF-POLLINATION OR CROSSING	PLACE: IN SITU OR EX SITU[a]	DATE OF POLLINATION	SUCCESS OF FERTILIZATION (%)[b]
WPM (25 plants selfed)	West coast, in situ	1 Feb.–10 Mar.	0
WPM (4 plants selfed)	East coast, in situ	1 Feb.–23 Feb.	0
cv. Wallis × WPM (1 plant)[c]	Pouembout, Exp. Field	23 Feb.	>90[d]
cv. PCT × WPM (1 plant)	Pouembout, Exp. Field	5 Feb.	72
cv. PCT × WPM (1 plant)	Pouembout, Exp. Field	23 Feb.	35
cv. PCT × WPM (1 plant)	Pouembout, Exp. Field	23 Feb.	46
WPM × Hybrid A (1 plant)	Pouembout, Exp. Field	1 Feb.	57
WPM × Hybrid B (1 plant)	Pouembout, Exp. Field	5 Feb.	38
WPM × Hybrid C (1 plant)	Pouembout, Exp. Field	12 Feb.	75
Hybrid D × WPM (1 plant)	Pouembout, Exp. Field	5 Feb.	85
Hybrid M × WPM (1 plant)	Wagap, Exp. Field	17 Feb.	14
Hybrid E × WPM (1 plant)	Pouembout, Exp. Field	18 Feb.	85
Hybrid F × WPM (1 plant)	Pouembout, Exp. Field	18 Feb.	75

[a] In the natural environment or in an experimental field.
[b] Estimated as the percentage of the number of developing fruits (berries) within the fruit cluster (the estimation took place about 2 weeks after controlled pollination and isolation).
[c] One plant of cv. Wallis was crossed with the wild morphotype (purple type).
[d] Percentage could not be determined exactly because unfertilized flowers were squeezed by fast-growing berries.

portion; the lower part of the spathe, which encloses the female portion, does not open enough; the constriction of the spathe in the sterile region between the female and the male portions of the spadix is too tight, so that pollen cannot reach the female portion; or the plants are self-incompatible. Self-incompatibility appeared to be the most important reason. Artificial self-pollination under isolation in naturally grown populations on the west and the east coasts indicated that the purple morphotype was self-incompatible and cross-compatible. Of 29 self-pollinated inflorescences, none showed any sign of a successful fertilization (Table 4). The green morphotype also appeared to be self-incompatible because no seed set was found in isolated, naturally grown populations, pollinated naturally and artificially.

Wild taro plants in Melanesia, with the exception of New Caledonia genotypes, are self-compatible and produce abundant seeds that germinate. It is consequently believed that local cultivars were probably introduced as clones to New Caledonia from Vanuatu, which is the hypothesized homeland of Kanaks. Most of these typical Pacific cultivars exhibit inflorescences with sterile appendices, similar to those of the wild Melanesian germplasm, but significantly different from those of wild New Caledonia genotypes, especially from the green morphotype. Elongated cylindrical suckers, similar to the cormels of *Xanthosoma sagittifolium*, also characterize the green morphotype, and this trait distinguishes it from Pacific taros, which are mostly dasheen types.

Our isozyme analysis indicated that New Caledonian wild genotypes are different from the wild types in Melanesia (Lebot and Aradhya 1991) and are not closely related to the existing local cultivars and other Pacific genotypes. It is very unlikely that birds or currents, considering the isolation of the island, were responsible for wild taro introduction to New Caledonia. They may represent remnants of an early domestication that took place long before the present traditional cultivars were introduced. Another possibility is that taro is an endemic element in the flora of Grande Terre. A similar hypothesis can be found in the discussion about the origin of Australian taro (Jones and Meehan 1989). They may represent remnants of the endemic

flora, a Gondwanaland heritage. New Caledonian wild germplasm can be used as an excellent source of genes for breeding, especially for improvement of adaptability to extreme environmental conditions. The green morphotype can be a good source for improvement of growth vigor.

ACKNOWLEDGMENTS

This study would not have been possible without the support of the INCO DC Programme of the EU, the French Ministry of National Education, Research and Technology; the Taro Network for Southeast Asia and Oceania (TANSAO); and CIRAD. We also thank Bénédicte Trilles for laboratory work at the French University of the Pacific and Jean-Emmanuel Perraud for organization of the fieldwork.

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